Effects of abiotic factors on plant-insect multitrophic interactions

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Chapter 1

General introduction

Introduction

In terrestrial ecosystems, plants represent the foundation of food chains that play an important role in mediating various interactions among organisms at various trophic levels. Species from the same and different trophic levels do not live in isolation, but they interact with each other at broad temporal and spatial scales. These biotic interactions, such as between plants and insects or between prey and predators, play a major role in determining the distribution and abundance of organisms (Van der Putten, Macel, & Visser, 2010; Wisz et al., 2013). Several studies have shown that such complex biotic interactions can play an important role in maintaining biodiversity and ecosystem stability and functioning (Mace, Norris, & Fitter, 2012; Van der Putten et al., 2010; Wisz et al., 2013).

Plant-insect interactions

In nature, plants are associated with many kinds of organisms that directly or indirectly influence community structure and ecosystem functions. The interaction between plants and insects is of crucial importance as both of them represent abundant groups in terms of species and biomass. Insect herbivores are one of largest groups among these organisms (Strong, Lawton, & Southwood, 1984). They play an important role in top-down control of plant biomass (Carson & Root, 2000). However, plants have evolved various defensive strategies, e.g. morphological and chemical traits which provide them with some protection against insect herbivores (Schoonhoven, Van Loon, & Dicke, 2005). For instance, plant trichomes are important morphological traits that confer physical defense against insect herbivores, and caterpillars often show preference for leaves without trichomes in the field (Fordyce & Agrawal, 2001). Plants also produce secondary metabolites (e.g. glucosinolates and phenolics) and volatile metabolites, especially when damaged by herbivores that directly or indirectly influence the performance and population dynamics of insect herbivores, altering their fitness through effects on e.g. survival, growth rate and body size (Karban & Baldwin, 2007; Takabayashi & Dicke, 1996; Van Dam, Hadwich, & Baldwin, 2000; Van Geem, Harvey, Cortesero, Raaijmakers, & Gols, 2015).

On the other hand, insect herbivores have evolved mechanisms to overcome the defensive traits of plants, such as the detoxification of secondary metabolites, and some specialist insect herbivores can even sequester defense chemical compounds for their own defense (Nishida, 2002; Scott & Wen, 2001). These adaptive mechanisms have enabled specialist insect herbivores to efficiently exploit the food plants on which they are specialized. Specialist herbivores often use a restricted number of host plants with similar classes of allelochemicals and are more efficient in coping with these plant defenses than generalist insect herbivores (Bernays, 2001; Mello & Silva-Filho, 2002). Generalist insect herbivores usually feed on a wide range of plant species but are less well able to deal with the chemical defenses of specific plant species (Ali & Agrawal, 2012).

Multitrophic interactions involving plants, herbivores, predator/parasitoids and hyperparasitoids

Plants do not only interact with insect herbivores, but they are also associated with insects at higher trophic levels such as parasitoids and predators (Hay, Pawlik, Duffy, & Fenical, 1989; Price & al, 1980). Parasitoids are insects that lay their eggs in or on the bodies of insect herbivores, and their larvae develop by feeding on the host (Godfray, 1994). Some predators, such as ladybeetles and birds, also intimately interact with insect herbivores and host plants (Both, Van Asch, Bijlsma, Van Den Burg, & Visser, 2009; Sentis, Hemptinne, & Brodeur, 2013). These tritrophic interactions in turn can be affected by species at the fourth or higher trophic level (Sullivan & Völkl, 1999). For instance, many parasitoids can be attacked by secondary hyperparasitoids that develop at the expense of the primary parasitoids (Harvey, Van Dam, & Gols, 2003; Sullivan & Völkl, 1999). Moreover, secondary hyperparasitoids may even be attacked by tertiary hyperparasitoids that use secondary parasitoids as their hosts (Brodeur, Hochberg, & Ives, 2000).

Effects of plant quality on the development of consumers at higher trophic levels

Plants play an influential role in mediating the behavior and physiology of the herbivores feeding on them. Herbivore growth and reproduction is influenced by primary metabolites, such as carbohydrate and nutrients (e.g. protein / nitrogen) levels present in the consumed tissues (Chapman & Chapman, 1998). In most diets of insect herbivores nitrogen is limiting (Mattson, 1980). Moreover, many plants produce a range of toxic secondary compounds that act as defence chemicals against insect herbivory (Karban & Baldwin, 2007). These compounds can act as feeding deterrents or significantly alter the physiology and development of herbivores, through reduced rates of growth, smaller adult size and increased mortality (Giamoustaris & Mithen, 1995). Reduced rates of herbivore growth on host plants with high levels of secondary defence chemicals can also result in an increase in development time that prolongs their exposure time or ‘window of vulnerability” to their natural enemies (the slow-growth-high-mortality-hypothesis, (Clancy & Price, 1987)). On the other hand, defence chemicals in host or prey diet may negatively affect the development and survival of their predators, parasitoids and even hyperparasitoids (Gunasena, Vinson, & Williams, 1990; Harvey et al., 2003; Heil, 2008; Ode, 2006; Soler, Bezemer, Van Der Putten, Vet, & Harvey, 2005).

Effects of abiotic factors (temperature, wind, rainfall) on species interactions

Many research linking plant chemistry to the performance of herbivores, pathogens and their natural enemies has been carried out under controlled conditions in which important abiotic factors, such as light and temperature, are fixed (Ode, 2006). Consequently, there is little information on how differences in abiotic conditions affect the development of consumers in a connected food chain. In addition to direct effects of abiotic factors on consumer development, we would also expect that changes in plant quality, mediated by abiotic factors such as temperature, wind and precipitation, affect the performance of species that interact in the food chains associated with the plant (indirect, bottom-up effects of abiotic factors on plant consumers). Moreover, we would expect that direct effects of abiotic factors on higher trophic level organisms, including natural enemies of consumers, affect the survival and development of lower trophic level consumers (indirect, top-down effects of abiotic factors on plant consumers). In this section, I will summarize how abiotic factors can affect herbivores and higher trophic level organisms either directly, or indirectly, i.e. mediated by changes in the quality of their hosts.

Direct effects of abiotic factors on insect herbivores

Abiotic factors clearly have direct effects on survival, behavior and development of insect herbivores. One major abiotic factor is temperature. The development of invertebrates, such as insects, is highly temperature-dependent because they are ectothermic and metabolism depends on ambient temperature (Castillo, Jacas, Peña, Ulmer, & Hall, 2006; Daane, Malakar-Kuenen, & Walton, 2004; Duale, 2005; Legrand, Colinet, Vernon, & Hance, 2004; Virtanen & Neuvonen, 1999). In addition to temperature, wind and rainfall are very important abiotic factors in nature. For example, wind can affect the movement and dispersal of insects (Speight, Hunter, & Watt, 2008). Another abiotic factor, rainfall, can remove herbivorous insects from their host plants via physical disturbance. These effects have been demonstrated e.g. by Kobori and Amano (2003), who showed that simulated rainfall washed off more than 80 % of the eggs of the diamondback moth from the upper leaf surface in one hour, and that the falling rate of larvae increased with increasing time of exposure to rain (Kobori & Amano, 2003). Furthermore, rainfall can also influence microclimate, which in turn affect development, behavior and population dynamic of insect herbivores (Dobkin, Olivieri, & Ehrlich, 1987; Kamata & Igarashi, 1994). Moreover, higher trophic level organisms such as herbivores are known to be more sensitive to short-term changes in climate than lower trophic level organisms such as plants, with significant effects on community structure and persistence (Bale et al., 2002; Voigt et al., 2003).

Indirect bottom-up (plant-mediated) effects of abiotic factors on insect herbivores

Abiotic factors can also indirectly affect insect herbivores through changes in plant morphological and chemical traits. Previous studies have shown that the development of insects can be influenced by effects of plant quality (bottom-up control) that cascade up the trophic cascade through their effects on herbivores and parasitoids (Bukovinszky, van Veen, Jongema, & Dicke, 2008; Harvey et al., 2003). Based on the empirical literature, it is now clear that rising temperatures can indirectly affect levels of herbivory via changes in primary plant chemistry and insect metabolism (Bale et al., 2002; Bidart-Bouzat & Imeh-Nathaniel, 2008). In addition to temperature, it has also been shown that wind and rainfall can indirectly affect the performance of insect herbivores via changes in plant quality (Cipollini, 1997; Shure, Mooreside, & Ogle, 1998). For example, plant exposure to wind resulted in increased chemical and morphological resistance against the two-spotted spider mite (Cipollini, 1997) and in reduced growth rate of the gypsy moth (Barbehenn, Haugberg, Kochmanski, & Menachem, 2015). By contrast, wind-exposure had no significant effect on the development rate of *Manduca sexta* (Cipollini & Redman, 1999). Rainfall can also indirectly affect the population dynamics of herbivores by changing concentrations in primary or secondary metabolites such as nitrogen and phenolics in the plant tissues that are consumed by the herbivores (Shure et al., 1998).

Indirect top-down (parasitoid/ predator-mediated) effects of abiotic factors on insect herbivores

In addition to their indirect bottom-up effects, abiotic factors such as temperature, wind and rainfall, can also indirectly affect herbivores through alteration of their top-down control by predators and parasitoids. Importantly, it has rarely been explored how climate warming, in particular heat waves, affects species interaction at the terminal end of food chains such as parasitoids (3rd trophic level) and associated hyperparasitoids (4th trophic level). Host exploitation behavior and competition in hyperparasitoids has been studied for decades (Harvey, Pashalidou, Soler, & Bezemer, 2011; Harvey, Wagenaar, & Gols, 2011; Hassell, 1971; Spataro & Bernstein, 2007). Thus far, many studies have been based on optimizing conditions for successfully rearing natural enemies of insect pests in biological control programs, whereas much less is known about processes affecting host-parasitoid interactions in nature. For example, temperature may have differential effects on development rate of organisms at different trophic levels (Berg et al., 2010; Franken, Huizinga, Ellers, & Berg, 2018). Therefore, the physiological and temporal synchrony between plants and associated organisms (e.g. herbivores, pathogens, natural enemies) are likely to be disrupted by elevated temperature. Nevertheless, few studies have investigated indirect top-down effects of wind and rainfall on insect herbivores. For instance, Barton (2014) demonstrated that wind exposure increased the density of aphids on soybean plants in treatments with exposure to wind in the field, and that the predation rate of these aphids by ladybeetles was drastically lower on plants in open (wind) plots than on plants in wind-blocked plots. Rainfall may also affect behavior and development of insect herbivores by influencing the foraging behavior of their natural enemies such as predators and parasitoids that is mediated by the volatiles emitted in response to herbivory (Dicke, 2016; Vallat, Gu, & Dorn, 2005). Therefore, understanding the mechanisms by which abiotic factors directly and indirectly influence the insect herbivores performance is important for predicting effects of climate change on insect communities and ecosystem functioning.

Effects of climate change on (multi)trophic interactions

A range of anthropogenic stresses is known to influence biodiversity in natural systems worldwide (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Walther et al., 2002). The 2014 Intergovernmental Panel on Climate Change (IPCC) report concluded that, because of the human combustion of fossil fuels and attendant increase in atmospheric levels of greenhouse gases, global temperatures are expected to rise between 1.4 and 5.8 °C in the coming century, with regional variations being much more extreme (IPCC, 2014). Seventeen of the 18 warmest years in the 136-year of global surface temperature record all have occurred since 2001, with the exception of 1998. The year 2016 ranks as the warmest on record (Source: NASA/GISS). Likewise, anthropogenic global warming (AGW) is driving changes in other climate-related factors, such as rainfall and wind change rapidly (IPCC, 2014; Vautard, Cattiaux, Yiou, Thépaut, & Ciais, 2010). Theoretical studies suggest that as many as 50% of species could become extinct by the middle of this century because of the effects of AGW on communities and ecosystems (Thomas et al., 2004). However, these predictions are mainly based on climate envelopes of individual species, without considering that species are linked by trophic interactions. Release from natural enemies could also make species more abundant. For example, insect outbreaks are predicted to increase in frequency and intensity with rapid regional increases in temperature through direct effects of climate change on insect populations and through the disruption of community interactions (Stireman et al., 2005). Consequently, there is an urgent need to explore effects of climatic variability on plant-insect and multitrophic interactions.

Objective of the thesis

The main aim of this thesis is to investigate how variation in abiotic factors influences the interactions involving four different trophic levels of organisms: plants, herbivores, parasitoids and their parasitoids. Although temperature is a major factor that affecting the interactions between plants and insect herbivores, other abiotic factors (wind and rainfall) also play an important role in regulating plant-herbivore interactions. Thus, in the first part of my thesis (chapter 2 & 3), I mainly examine effects of wind and rainfall on the performance of insect herbivores feeding on plants. In the second part of my thesis (chapter 4 & 5), I explore how temperature variability affects reproduction and competition in higher trophic levels (hyperparasitoid) to understand the mechanisms involved in how climate warming, in particular heat waves, influence species interactions at higher trophic levels (parasitoid-hyperparasitoid). In this thesis, I study effects of abiotic factors on multitrophic interactions involving a naturally occurring plant species, *Brassica nigra,* and its associated herbivores, predators/parasitoids, and hyperparasitoids (from the 1st trophic level up to the 4th trophic level, Figure 1).

Model system

The model plant in my thesis is black mustard, *Brassica nigra* L. (Brassicaceae) a cruciferous plant, which is widespread over much of Eurasia and is native to the Netherlands. This plant species is common in a range of climatic regions, including hot regions of southern Europe (e.g. the Mediterranean basin) and cooler regions of central/northern Europe; here we used seeds originating from populations in the Netherlands. It is an early successional species that exploits a range of habitats and grows in densities ranging from single plants to populations consisting of many thousands of individuals. Like other members of its family it produces secondary compounds known as glucosinolates (GS) which have been shown to act as feeding deterrents or to exhibit negative effects on the growth and development of generalist insect herbivores (Bezemer, Wagenaar, Van Dam, & Wäckers, 2003; Wardle, Bonner, & Barker, 2000). However, many specialist herbivores including species used in my thesis are evolved to be less affected by secondary metabolites of their host plants.

We focused on interactions involving two specialist lepidopteran herbivores of brassicaceous plants that produce GS. The large cabbage white butterfly *Pieris brassicae* L. (Lepidoptera: Pieridae) is a widespread species found across much of Eurasia (Feltwell, 1982). Larvae of *P. brassicae* have been regularly observed feeding on wild populations of *B. nigra* (Harvey et al., 2003). Female *P. brassicae* lay up to 100 eggs in cluster (Davies & Gilbert, 1985). Larvae go through five instars during development before entering the pupal stage. This species generally has two generations in the Netherlands, but can also have three generation in a warm year (Fei, Gols, & Harvey, 2014). The diamondback moth *Plutella xylostella* L. (Lepidoptera: Plutellidae), the other specialist herbivore used in this study, is one of the most destructive members of the insect pest community that attacks *Brassica* vegetable crops in various parts of the world (Furlong, Wright, & Dosdall, 2013). Adult females can oviposit up to 300 eggs. Larvae go through four instars, and feed as leaf miners during their first instar (Capinera, 2000).

Cotesia glomerata L. (Hymenoptera: Braconidae) is a gregarious, koinobiont endoparasitoid that attacks young larvae of *P. brassicae* (Feltwell, 1982). Adult female wasps typically lay 10-40 eggs into L1-L3 larvae of *P. brassicae*, and the parasitoid larvae develop within the growing host caterpillar. After parasitoid larvae emerge from their host caterpillar, the caterpillar dies and the larvae spin a cocoon from which they emerge as adult wasps. I only use this parasitoid species to study the effects of heat waves on reproduction and competition of its hyperparasitoids (species described below). The great tit (*Parus major*) is a passerine bird in the family Paridae. It is a widespread and common species in Eurasia, where it is found in a variety of forest and forest-edge habitats. During the breeding season, its diet consists of a wide range of small invertebrates, including caterpillars that it hunts from among leaves and branches.

Gelis agilis Fabricius (Hymenoptera: Ichneumonidae), *Acrolyta nens* Hartig (Hymenoptera: Ichneumonidae) and *Lysibia nana* Gravenhorst (Hymenoptera: Ichneumonidae) are idiobiont hyperparasitoids at the fourth trophic level (secondary parasitoids) that attack *C. glomerata* cocoons, kill the host larva inside the cocoon, and consume it. *G. agilis* is an asexually reproducing generalist species whose females are wingless, whereas *A. nens* and *L. nana* reproduce sexually and adults are fully winged and specialist (Harvey, Wagenaar, et al., 2011; Harvey, Wagenaar, & Martijn, 2009). Moreover, *G. agilis* and the other two hyperparasitoids exhibit quite different reproductive and host utilization strategies. All of the three species emerge as adults with no mature eggs. However, adult female *G. agilis* obligatorily feed on host haemolyph for egg production and mature eggs slowly and only in very small numbers (4 eggs on average), whereas *A. nens* and *L. nana* do not host feed and mature eggs more rapidly and in larger numbers (~ 40 eggs on average) (Harvey, 2008; Harvey et al., 2009).

Thesis outline

In **chapter 2**, I investigate the direct and indirect (plant-mediated) effects of wind on the development and survival of insect herbivores on *B. nigra* plants. In a greenhouse experiment, plants infested with herbivores (*P. xylostella* and *P. brassicae*) are exposed to different wind regimes and their performance is assessed under different wind conditions. Based on the results obtained, I further conduct a behavioral experiment to examine whether wind reduces the predation risk of caterpillars of the macrolepidopteran species (*P. brassicae*) by an avian predator, the great tit (*Parus major*).

In **chapter 3**, I investigate the direct and indirect effects of different rainfall patterns on the development and survival of insect herbivores on *B. nigra* plants. In a greenhouse experiment, plants infested with or without herbivores (*P. xylostella* and *P. brassicae*) are exposed to different simulated rainfall treatments. Furthermore, I test whether the frequency and duration of rainfall affect the performance of the insect herbivores.

In **chapter 4**, I investigate the effects of simulated heatwaves on reproduction and functional responses in two hyperparasitoid wasps, *A. nens* and *G. agilis* in host cocoons of a primary parasitoid, *C. glomerata*. Survival of host cocoons and host exploitation success by hyperparasitoids are compared at different temperature regimes. In addition, I examine the effects of host quality (cocoon age) and hyperparasitoid physiological condition (female age and nutritional status) on exploitation success, as they are important biological factors that can affect the host exploitation behavior of both hyperparasitoids.

In **chapter 5**, I investigate how temperature variability affects intrinsic competition between two hyperparasitoids, *L. nana* and *A. nens* in host cocoons of a primary parasitoid, *C. glomerata*. Host cocoons are parasitized by both species at different time intervals and are exposed to three different day and night temperature regimes.

Lastly, **in chapter 6**, I discuss the main results of my thesis in the context of multitrophic interactions under climate change scenarios. I emphasize the importance of abiotic factors, in particular with regard to wind, rainfall and temperature, in the studies of plant-insect and multitrophic interactions, as well as the importance of higher trophic levels in projecting the ecological effects of climate change.

An overview of the thesis is given in the diagram below (Figure 1).

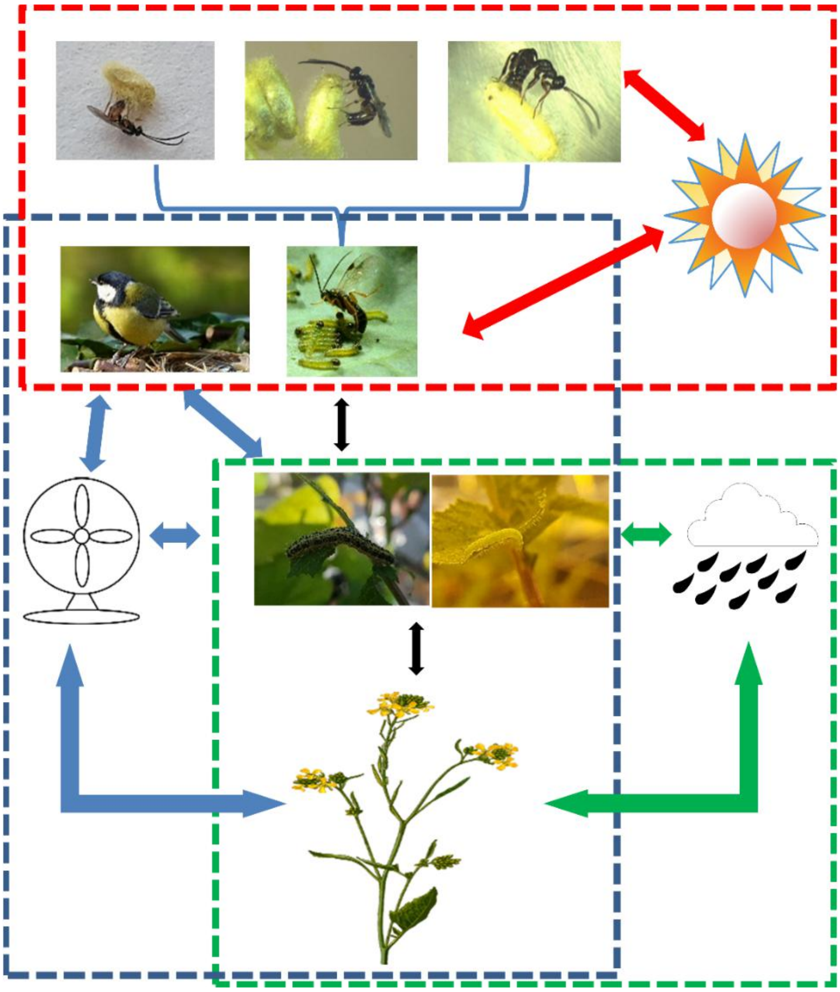

Figure 1. Diagram of a natural study system involving four trophic levels. The blue box illustrates organisms and factors studied in chapter 2, including the plant species, *Brassica nigra*, and two herbivore species, *Pieris brassicae* and *Plutella xylostella*, that are used to study the effects of wind on herbivores performance as well as the avian predator species, *Parus major* that is used to test the effects of wind on predator preference. The green box illustrates organisms and factors studied in chapter 3, in which I examined the effects of rainfall on the two herbivore species described above. The red box illustrates organisms and factors studied in chapter 4 & 5, including a parasitoid species, *Cotesia glomerata*, and three hyperparasitoid species, *Gelis agilis*, *Acrolyta nens* and *Lysibia nana*, that were involved in studies on the effects of simulated heatwaves on parasitoid-hyperparasitoid interactions.